ON THE OSTEOLOGY AND SYSTEMATIC POSITION OF THE PYGOPODES.

R. W. SHUFELDT.

In a series of papers contributed to *The Journal of Anatomy and Physiology* of London (1889–1890) appeared a number of my drawings of the bones of pygopodine birds. Among these the osteology of certain grebes and loons was illustrated, but the material at hand then was meagre. Moreover, through an oversight the plate illustrating the bones of the lower extremity in the loons was omitted. The osteology of the pelvic limb in a loon is in a way more deserving of our consideration than perhaps other parts of the skeleton in those typical divers, and as I had fortunately preserved the aforesaid plate, I take occasion to publish it here.

In an article entitled "Concerning some of the Forms assumed by the Patella in Birds" (*Proc. U. S. Nat. Mus.* Vol. vii, 1884, pp. 324–331) I published two or three figures of the leg-bones in loons and grebes, but the descriptive text-matter had reference only to the morphology of the patella.

In the present memoir all of my previous work has been amplified and practically rewritten, while I have added my investigations upon the osteology of the Pygopodes.

In my classification of birds the Pygopodes appear in the scheme as a suborder, thus: —

Suborder: — PYGOPODES.

SUPERFAMILIES: —

Podicipoidea.

Urinatoroidea.

FAMILIES: —

Podicipidæ.

Urinatoridæ.

Newton in his classic 'Introduction' to his *Dictionary of Birds* (p. 111) makes the statement that the "group known as *Pygopodes* has been often asserted to be closely akin to the *Impennes*, and we have seen that Brandt combined the two under the name of *Urinatores*, but of their essential difference there can now be no doubt, and indeed it is hard to look upon *Pygopodes* as a natural group, so many are the differences between the *Podicipedidæ* or Grebes and *Colymbidæ*[1] or Divers, though recent morphologists agree to unite them, while the affinity of the Divers to the Auks seems to be still more uncertain, and there appears to be ground for considering the *Alcidæ* to be much modified relatives of the *Laridæ*."

The discovery of the toothed Hesperornithidæ of the middle cretaceous of America has doubtless modified the opinions of systematists regarding the affinities of the Pygopodes.

I agree then essentially with Fürbringer in confining the families Colymbidæ (loons) and Podicipidæ (grebes) to a group "Colymbo-Podicipites," and closely associating the latter with the families Enaliornithidæ and Hesperornithidæ in a Suborder Podicipitiformes. Therefore I can proceed to the consideration of the osteology of the grebes.

THE SKELETON OF THE GREBES.

Grebes may have the superior osseous mandible longer than the cranium, or they may have it shorter than that part of the skull. Of the first-mentioned, *Colymbus holbœlli* is a good example, while *Podilymbus podiceps* exhibits the latter characteristic. In *C. holbœlli* the long, straight and acutely-tapering superior osseous mandible is fully one fourth longer than the cranium, and either narial aperture is suboval in outline, being equal in length to the end of the bill which extends beyond its anterior termination. This narial aperture is rather acutely holorhinal posteriorly, and the dentary margins are cultrate for

[1] "American ornithologists have lately used this term for the Grebes, to the great disturbance of nomenclature. It is apparently from the ancestors of the *Colymbidæ*, before they lost their teeth, that *Hesperornis* branched off as a degenerate, bulky and flightless form." — A. N.

their entire extent. No part of the nasal septum ossifies in the skull (a feature common to all grebes that we have examined). Each nasal bone has a form much as we find it in the loons, its processes being flat and rather broad. The region over the cranio-facial hinge is moderately concaved, where the nasal processes of the premaxillaries are seen to be persistent throughout life, and their sutures plainly visible in the adult.

Posterior to this space the frontals between the superior orbital margins are much narrowed, and the supraorbital glandular depressions barely discernible, being distinguishable in the dried cranium only along their posterior moieties. The external superficies of the cranial vault in the parietal region are smooth and rounded; the crotaphyte fossæ are extensive and practically meet, mesially, over the large rounded supra-occipital prominence, though no median crest or line stands between them. More laterally, and upon either side, the occipital crest is raised and prominent. In the grebe now under consideration it is quite as thin, and lamellar-form as it is in the loons.

Upon lateral aspect of the skull, the post frontal and squamosal processes are much absorbed, and the valley between them wide. The aural entrance is extensive, very open and exposed, being overarched by its somewhat thickened postero-superior border.

Either zygomatic bar is straight, transversely flattened, and tapers slightly as it proceeds forwards where it assists in making a schizognathous articulation with the other bones.

The interorbital septum is markedly deficient in bone, and the anterior cranial walls about the exit of the nerves hardly less so. This deficiency is even greater than it is seen to be in the loons. Pars plana is weak and feebly developed, and externally, it passes upwards and forwards to fuse with the nether aspect of the frontal. A transverse perforation may normally exist just posterior to the true mesethmoid. This latter ossification terminates rather abruptly in front by a broadish face with a small median crest extending down it as far as the sharpened anterior apex of the rostrum, over which it is carried forwards.

A lacrymal is a fair-sized bone with a very narrow superior limb, closely articulating with its entire mesial border with the

frontal and nasal, while the rather larger descending portion of the bone is plate-like, being transversely compressed, and does not reach the maxillary below. At its apex it supports a spiculiform os uncinatum, as we find in the Urinatoridæ.

The foramen magnum is large, looks almost directly backwards, and is of an acute cordate outline, with the apex above. The occipital condyle is well developed, completely sessile, and barely notched superiorly. Passing to the basitemporal area we find it somewhat contracted, nearly level and smooth, while its anterior apex underlapping the double entrance to the Eustachian tubes. There are no evidences whatever of basipterygoid processes, and the long, straight pterygoids stand well away from the sphenoid. One of these bones has cultrate inner and outer edges or borders, and is peculiar in the way it articulates with the quadrate. The latter bone throws out a well developed apophysis, mesially, the summit of which is rounded to be received into the articular cup existing on the posterior end of the pterygoid. In most birds the pterygoids articulate upon the inferomesial border of the os quadratum. These bones in the grebe hardly touch each other anteriorly, where their palatine heads are to some extent expanded. The sphenoidal rostrum is comparatively slender and is carried to a sharp apex in front. The palatines have their postero-external angles completely rounded off, while their lower inner and outer margins are moderately bent downwards,— the inner one rather abruptly so. When articulated *in situ* these bones are in contact with each other all along beneath the rostrum. The antero-mesial portion of the post-palatine part of the bone, curls upwards and inwards towards the mesethmoid, and in front its mesial process runs forward as a long slender spine for the accommodation of the vomer. The prepalatine portion of a palatine is long, narrow and vertically compressed. Extending a long ways to the front, rapidly tapering to a point as it does so, the prepalatine underlaps the maxillary and maxillo-palatine, and passes along close to the inner aspect of the dentary part of the premaxillary, being thoroughly fused there in the adult. The suture, however, remains visible throughout life. For the size of the bird, Holbœll's grebe has one of the longest vomers at present

known to me. It is lamelliform, thin and narrow, its surface being in the middle plane, while behind it is moderately bifurcated, to be carried to a sharp apex anteriorly. Either maxillo-palatine is a subconcavo-convex oval plate of bone, of some little size. Its mesial surface looks inwards and upwards, the anterior fourth being fused almost indistinguishably with the nasal, maxillary, palatine and premaxillary. Palatines and maxillo-palatines are well separated from each other in the middle line, and from the vomer.

An os quaratum is rather a large bone in the grebes, with a long, gently-inturned orbital process. Its mastoidal head supports two facets of articulation, being separated from each other by a shallow sublongitudinal valley. Transversely, the quadrate is much compressed, and I have already described above the process at its infero-internal angle to accommodate the hinder end of the corresponding pterygoid. The mandibular portion is much excavated centrally on its nether aspect, with a small articular facette on either side of the concavity. There is also an articular line bounding this depression posteriorly. The bone appears to be pneumatic.

Passing to the consideration of the mandible we find it to be of the very acutely V-shaped pattern, with the ramal vacuity completely closed in. The articular ends are enlarged and abruptly truncated behind, where they show each a flat triangular surface. The ramal sides posteriorly are thin, lofty and flat, to become narrower and thicker as they pass tapering forwards to the acute apex. The symphysis is short, slightly excavated above, and rounded below. It is only the posterior extremities of the mandible that are at all pneumatic, the usual pneumatic orifice being at the end of the inturned, stumpy articular termination of the bone. Aside from the brevity of the superior osseous mandible in the short-billed grebes, the skull characters as given above for *Colymbus holbœlli* are substantially repeated in them. In *Podilymbus podiceps*, however, I observe that the anterior extremity of the vomer terminates in a small, rounded, disc-like nib, and its quadrates are rather more delicately fashioned. It also has the mesial notch on the upper side of the occipital condyle, and a mid-longitudinal raised line on the supra-

occipital prominence, which, as we shall see, is so much better marked in the loons. Finally, the supra-orbital glandular depressions are hardly perceptible in these dabchicks.

Grebes possess a hyoidean apparatus in some respects peculiar. It is well exemplified in Podilymbus, where we find the glossohyal performed entirely in cartilage, and the first basibranchial represented by an expanded suboval disc of bone. At the hinder margin of this the short second basibranchial, as a delicate osseous rod, articulates in the middle line, while the long, slender cerato-branchials, one on either hand, articulate close to it. The epi-branchials are short and spiculiform. We find a somewhat similarly fashioned first basibranchial in the tongue of the kingfishers, but such a form of it is rare among birds.

The sclerotal plates in the eye-balls of the Podicipoidea have their usual ornithic characters, being of moderate size only, squarish in form, and overlapping each other in the ordinary manner.

THE TRUNK SKELETON IN THE GREBE.

Birds of this superfamily vary, even for the genera, with respect to the number of vertebræ in the spinal column, and the corresponding vertebræ themselves vary much in form and character. Species such as *Colymbus holbœlli* and *Podilymbus podiceps* have 19 vertebræ in the cervical region of the spine, the 19th bearing a pair of ribs that do not articulate by costal ribs with the sternum.

But *Æchmophorus occidentalis* has 21 vertebræ in the cervical region, with the free ribs on the 21st as they occur on the 19th in Podilymbus. This last mentioned species has the first four dorsal vertebræ fused into one piece, but the fifth one, standing between this piece and the pelvis is free, and its ribs articulate with the sternum by costal ribs. There is also a pair of pelvic ribs, the hæmapophyses of which do not usually meet the sternum. All have large epipleural appendages, save the last-named; they being even found on the cervical pair. They do not fuse with rib borders.

In Æchmophorus the dorsal vertebræ do not fuse, although

the interarticulations are very close. This grebe has *two* pairs of pelvic ribs, the hæmapophyses of the first pair reaching the costal borders of the sternum. All grebes have large hypapophyses on the last two or three cervical vertebræ, and on all the centra of the dorsal vertebræ; they are very large in Æchmophorus, the first two being represented by flattened and out-spreading discs of bone of an irregular form. This species is also peculiar in having the neural spines of the 19th, 20th and 21st vertebræ much modified for muscular attachment. They resemble the ploughshare in form, being greatly increased in size, and the excavation occurring behind. The first (19th) has this modification most pronounced, while it is least marked in the ultimate one (21st). Parapophysial spines are quite aborted, or are represented by mere nibs of bone. Æchmophorus has the hypapophysial carotid canal extending through *twelve* vertebræ; it being generally closed in completely on the 9th and 10th one of the series. These vertebræ are the 4th to the 15th inclusive.

In *Podilymbus podiceps* I found 49 vertebræ in the spinal column. Nine free vertebræ and a pygostyle compose the tail of this bird, and when they are articulated *in situ*, they form a peculiar sigmoid curve, dipping downwards, then upwards, as the letter S. The pygostyle is very small and its characters much aborted.

Grebes have their caudal vertebræ considerably compressed in the transverse direction. In the dorsal region the tendons of the spinal muscles ossify and fuse with the summits of the neural spines of the vertebræ, and metapophysial spiculæ may also occur upon the transverse processes, as we find them in other water birds. Another thing is worthy of attention here, and that is the general form and outline of the skeletal parietes. Further along it will be seen that in the auks and puffins this is elongated,— the sternum being long, and the ribs sweeping far backwards beneath the pelvis. In the grebes this is not usually the case, for in Podilymbus the form of the thoracic skeleton is much as we find it in the gulls; in Æchmophorus, however, it is again more as in the Alcæ; it is quite so among the loons.

The form assumed by the pelvis among the Podicipoidea is

noteworthy; though in its general pattern it closely approaches what we find in the Urinatoridæ. The pelvis in *Æchmophorus occidentalis* well exhibits all the characters of this compound bone among the podicipidine types. In that species is much elongated and compressed laterally, especially its pos-acetabular portion. In front of the acetabulæ the fused sacral crista rises far above the fore part of the ilium on either hand,— which latter, each have the form of an oar-blade with a squarely truncated anterior extremity. An extensive antitrochanter surmounts either cotyloid cavity, while posteriorly the post-acetabular surface faces almost directly outwards. Along the dorsal middle line, for the posterior third, of the pelvis the iliac borders are closely pressed together, marking the uro-sacral vertebræ. Behind, a deep cleft indicates the division which originally marked the terminal point of union between the ilium and the very long and narrow ischium. The obturator foramen completely merges with the obturator space, and the much-extended, flat, ribbon-like post-pubic rod is widely separated from the lower ischiac border, being carried far back almost opposite the pygostyle. The ends of these bones of the pelvis, however, are not dilated as are the postpubic bones in the loons. The ischiac foramen is large, and of an elliptical outline. Podilymbus presents almost the same pelvic characters as those just described for Æchmophorus, and in this species the os innominata fuse completely with the "sacrum,"— though posteriorly the superior iliac margins do not quite meet over the uro-sacral vertebræ.

The sternum is very characteristic. In Figures 1, *a* and 1, *b* I have drawn it for *Colymbus nigricollis californicus* where its podicipidine features may be seen. Generally speaking it is broad and short, with a large subelliptical notch cutting out its xiphoidal portion on either side of the keel. This gives rise to a pair of flaring external xiphoidal processes, which curve outwards, then inwards, extending rather beyond the mid-xiphoidal prolongation. They are long and narrow in the short-billed grebes, and broader and relatively shorter in Æchmophorus and Colymbus. The mid-xiphoidal process always shows a triangular notch, which is much deeper in Podilymbus than in other species,

and it may also show certain foramina in the hinder part of the sternal body. The keel is triangular with a somewhat acute carinal angle produced in front, and closely approached by the os furcula when the bones of the shoulder-girdle are articulated *in situ*. Usually *six* articular facettes are found upon either costal border, and a costal process is large and subtriangular. No manubrium exists, and the bone is depressed where it occurs in the sternum when it is present. The costal grooves are noteworthy, for they are very deep, and their superior and inferior borders are produced well forwards.

As in the rest of the skeleton, save the hinder part of the skull and lower jaw, the sternum in the grebes is completely non-pneumatic.

Upon comparing the sterna of our various species of grebes, I find but few characters of marked difference beyond the matter of size. *Colymbus auritus* possesses a sternum most like that of *Podilymbus podiceps*, and next to it, in that respect, comes *Colymbus holbœlli*.

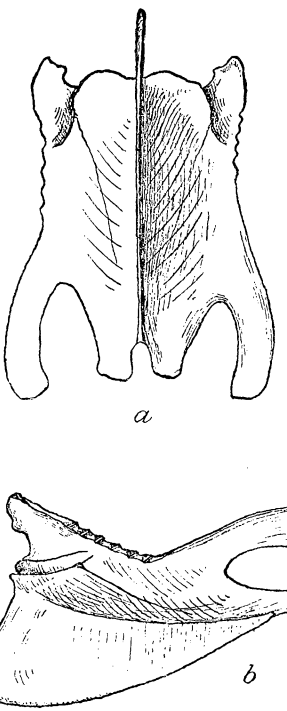

FIG. 1, *a*. Sternum of (*C. n californicus*) from below; *b*, left lateral view of the same bone. Natural size.

In the several bones of the shoulder-girdle, — the salient characters are the same for the various species of this group. The os furcula is always found to be of the broad U-pattern, much bowed to the front, without hypoclidium (*C. n. californicus*), and with narrow, laterally compressed limbs. Superiorly, the clavicular limbs taper out to acute points, and when the elements of the girdle are articulated *in situ*, one of these rests by its outer

aspect against the head of the corresponding coracoid, while the apex passes far over the anterior end of the scapula. Thus a piece of the clavicular end, including the apex, is above the scapula but not being in contact with it; — the actual point of contact between these two bones being several millimeters beyond or anterior to the apex.

The scapulæ are quite long, and narrow, being gently curved throughout their length in the vertical plane, the convexity being along the dorsal aspect. For the most part the bone is of uniform width, the head alone being somewhat thickened. It offers only a moderate articular surface for the coracoid, and the os furcula rests upon its upper side.

The scapulæ are especially slender in *Colymbus auritus*. Comparatively speaking, the coracoids are usually long and not very stout; they may, however, be only of moderate length. The summit of one of these bones offers us the usual ornithic characters, being peculiar only in having such a small scapular process, and being rather compressed laterally. The distal end of the bone is dilated and much flattened in the antero-posterior direction. This expansion is carried some distance up the outer side of the shaft, and, owing to the fact that the sternal end of a coracoid sets so deep in its articular groove in the sternum, the corresponding articular surface on the bone is carried up some little distance both in front and behind,— most so upon the latter aspect.

When the bones of the shoulder-girdle in a grebe are articulated as in life, there is quite an interval between their sternal ends, mesiad. As I have said above, this interspace on the sternum is concave and its convexity is coextensive with the inner border of the coracoid upon either side. A wide interval in the same location exists in *Hesperornis regalis*, the great diver of the Cretaceous epoch in America.

THE APPENDICULAR SKELETON OF THE GREBES.

As an example of the skeleton of the pectoral limb of an adult specimen of *Colymbus holbœlli* we have chosen No. 17815 Coll. U. S. Nat. Mus. In this specimen the humerus is 10.6 cms. long, with nearly a straight, subcylindrical shaft, the extremities

of which are but moderately enlarged. At the proximal end the radial crest is seen to be much reduced, and the excavation overshadowed by the low ulnar crest which is unusually shallow, with no evidences of pneumatic orifices. The articular surface of the humeral head has the ordinary avian character. Distally, the oblique and ulnar tubercles are prominent and offer considerable articular surface for the antibrachial bones. The ulna is 10.2 cm. in length, and considerably compressed subtransversely; the long, slender radius when articulated, *in situ*, with it, is in contact with its shaft for its distal moiety, thus much reducing the "interosseous space," which, in reality, only exists proximally. Manus has a total length of 8.3 cms., and the two usual free carpals are present in the wrist. Carpo-metacarpus is peculiar in being so comparatively long and slender, and for having the index and medius metacarpals so close together, and so nearly parallel. The phalangeal digits are long and slim, and I fail to find any "claws" upon the distal extremities of any of them. The proximal phalanx of the index digit is also elongated and remarkably narrow; the expanded portion and digital shaft being indistinguishably merged with each other.

The skeleton of the wing in *Podilymbus podiceps* has the same essential characters as in the wings of the long-billed grebes. In all, the bones are well-proportioned and harmonize in their lengths and calibres with the bones of the pelvic limb, in any given species.

Altogether one of the most beautiful adaptive structures is the pelvic limb of a grebe. When properly articulated, the short femur has its long axis directed from the acetabular center, downwards, outwards, and slightly backwards. By the structure of the knee-joint this brings the long axis of the tibio-tarsus almost parallel to the long, mesial axis of the pelvis. Now the tibio-tarsal articulation permits the exact play of the foot, by a fore and aft motion, at right angles to this long axis of the tibio-tarsus. It is an avian oar. The tarsus is compressed to the last degree consistent with strength, — so that when it and its blade-like toes make the forward stroke, the minimum amount of podal surface is offered to the water in resistance. But in the backward stroke of the foot, the articulation permits of the

reversal of this act, and the toes being turned, and to some extent the tarsus, the maximum amount of surface thus afforded is brought into play as in an oar. Femur and tarso-metatarsus have about equal lengths, and they each equal *half* the length of the leg-bones, measuring from the apex of the patella to the mid-lower point of the arc of the distal tibial condyles (*Podilymbus podiceps*). The mid-anterior toe in the adult measures 5.5 cm. and the tarso-metatarsus only 3.8 cm.; these are about the usual proportions.

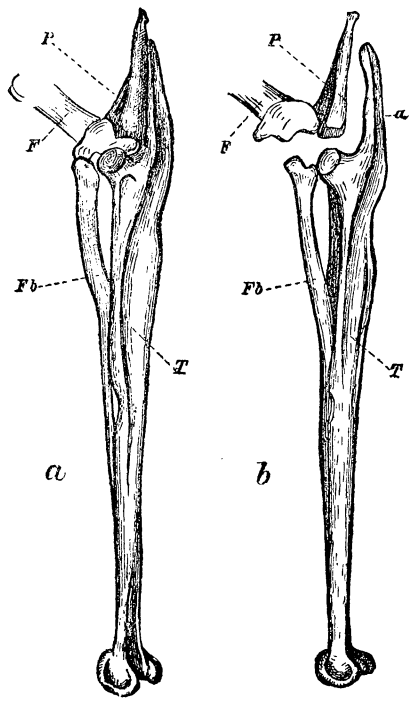

FIG. 2.— Leg-bones and patella of *Colymbus auritus*. *a*, the limb rotated slightly outwards; *b*, a square lateral view. In *a* the bones are *in situ*; in *b*, femur and patella are thrown backwards out of position. *a* rotular crest of tibia. P, patella; F, femur; *Fb*, fibula; T, tibio-tarsus. Natural size.

The head of the femur is large, and much excavated for the round ligament. At the summit the articular surface is rounded, and the trochanter does not rise above it. Its shaft is very slightly bowed to the front, and its condyles markedly prominent behind, with an unusually distinct and gaping cleft for the head of the fibula.

One of the most important characters of the tibio-tarsus is the upward extension of its cnemial crest, which is carried up to an apical process considerably above the summit of the shaft, but in direct line with the forepart of it. A large patella backs this at its supero-external aspect. It has something of the same form as the cnemial crest, above which it is slightly extended when articulated *in situ*. The procnemial ridge of the tibio-tarsus is extended as a sharp border down the

shaft of the bone; the latter being straight, flat anteriorly and rounded behind. Having the usual ornithic form, the tibial condyles are set rather obliquely on the distal end of the shaft. They are about parallel to each other. The fibula is very long with its lower end fused with the side of the shaft of the tibia. Superiorly, it is broad and flattened in the antero posterior direction, and stands well away from the tibial shaft (Figs. 2, *Fb.*).

Among the short-billed grebes the transverse compression of the shaft of the tarso-metatarsus is not nearly so evident as it is in such species as *Æchmophorus occidentalis* and *Colymbus holbœlli*. Moreover, in the dabchick there is a very slight twisting of the shaft upon itself, and this I have not observed in other grebes, either fossil or recent. At the summit of the bone, the articular excavations for the tibio-tarsal condyles are deeply sculpt, and the inner lateral border of the internal one may be conspicuously raised (Podilymbus). The subcubical hypotarsus of the tarso-metatarsus in most all grebes is deeply once-grooved in the mid-longitudinal line behind; and in front of this groove it presents one complete cylindrical perforation (also for the passage of tendons) with a similar, though smaller, perforation upon either side of it, situated more posteriorly.

This is quite different from what we find in the loons (see Fig. 18, of the Plate). Of the distal trochleæ the middle one is the lowest on the shaft; the outer one next; while the inner one is very distinctly elevated. They are all more or less drawn towards the rear aspect of the bone. The hallux digit is feeble and flake-like, as is the small, free metatarsal to which it is attached. It is considerably elevated upon the shaft.

Generally, the podal joints show more or less compression, while the terminal or ungual ones are positively scale-like, and, as it were, greatly flattened. Usually, the basal phalanges are the longest, and the others in any toe gradually diminish in this particular proceeding towards the extremities. Their arrangement as to the number on each toe is upon the more common ornithic plan of 2, 3, 4, 5 to the 1–4 toes respectively.

THE SKELETON IN THE LOONS.

In all of its essential characters, the skull of the loons agrees with that of the grebes. In the present description I have chosen the skeletons of *Urinator imber* and *Urinator lumme*,—the first being the bird known all over the world as *the* loon, the second, also a largely cosmopolitan type, is the red-throated loon or diver. In the latter the superior osseous mandible is fashioned upon the same plan as we found it in the long-billed grebes; it differs principally in curving very gently upwards, a feature not present in the beak of *U. imber*. The culmen in both species is convex and evenly rounded. Loons have the cranio-facial region depressed, best seen in *U. imber*, where the sutures between the nasal processes of the premaxillary and the nasals remain more or less open throughout life.

All the Urinatoridæ are holorhinal, and the dentary process of the nasal dips downwards and forwards in a gentle curve, thus including the large and somewhat elliptical osseous nares. They are devoid of any osseous nasal septum. Each lacrymal articulates to a very limited extent with the corresponding frontal, and almost entirely with the outer margin of the nasal. The os uncinatum at the inferior apex of its descending limit, fuses with that bone, but the lacrymal does not reach down to the maxillary in *U. lumme*, although it often does so in *U. imber*. In many of the gulls this process is much shorter, and is bent backwards and often anchyloses with the pars plana; in the Urinatoridæ the pars plana is not ossified, and the meseth-moidal plate is thin, showing a raised welt at the usual site of the base of this wing where it occurs in other groups.

A large vacuity is seen in the middle of the interorbital septum, but the optic and other foramina usually retain their integrity. The track of the olfactory nerve is commonly roofed over for its posterior third or more by an extension of the bony wall which covers the anterior aspect of the rhinencephalon. This arrangement is not seen in a specimen of the skull of *Larus glaucus*, and its interorbital septum is thick and entire.

The quadrate has a long, plate-like, and upturned orbital proc-

ess, and two prominent facets upon its mandibular foot, at about the same level.

Regarding the skull of any of the Urinatoridæ from above, the most striking features are the deep, sharply-defined, supra-orbital glandular depressions. These are extensively perforated by minute foramina over their posterior halves, while a large irregular foramen occurs at each anterior end. Over the frontals they are separated by a thin crest of bone in the median line, while their posterior halves curve regularly outwards, to extend upon each roof-like post-frontal projection. In *U. imber* we find them giving rise to a raised superior orbital margin, connecting the lacrymal and the aforesaid post-frontal projections, as in Alca and Uria. In *Urinator lumme* this rim is sometimes incomplete. Fully as marked as these supraorbital depressions are the extraordinary crotaphyte fossæ. These are very broad antero-posteriorly, and strongly-marked throughout. On the top of the skull they are separated by a raised median line of bone, being the simple backward extension of that smooth central area of the vault, which has remained unmutilated by depressions. From this these fossæ sweep on either side in increasing depth downwards and forwards beneath the overhanging post-frontal roof and over the top of the external auditory wing.

In a specimen of *U. imber* belonging to the U. S. National Museum (No. 18256) I find the superficies of the superior orbital margins very much roughened. In the middle line there is also a "parietal foramen" at the hinder termination of a longitudinal gutter that extends as far forwards as the thin crest dividing the supraorbital glandular depressions.

Viewing the skull of the red-throated diver from behind we find that the large dome-like supra-occipital prominence is overlapped by these broad crotaphyte fossæ, and the median line separating them is extended directly backwards as far as the superior margin of the foramen magnum. This prominence is also transversely crossed about its middle by the raised crest that separates the crotaphyte fossæ from the occipital area. The plane of the foramen magnum is nearly vertical, and the reniform condyle projects directly backward from a thick-set

pedicle, its convex surface being inferior. We shall see further on that this posterior aspect of a diver's skull resembles much less the same view of the skull of any of the Laridæ than Alca does; indeed, the posterior view of the skull of the razor-bill very closely resembles a like view of the skull in several of the gulls.

On the under side of the skull of *Urinator lumme* we find the arrangement of the palate and other elements agreeing in all essential particulars with the gulls, auks, or guillemots; in other words, its structure is that of a typical cecomorph of Huxley's classification, so far as these parts are concerned.

In a well-cleaned skull the palatines can easily be traced to their anterior endings, and this is equally true of *U. imber*. Behind they are long and narrow, showing a double carination with a concavity dividing them. This is again divided by a transverse ridge near the middle of the body of each bone on its under side. The ascending processes of the palatines are embraced by the hinder ends of the vomer, and between them both rides the thin inferior edge of the rostrum. Anteriorly the vomer among the Urinatoridæ is more or less pointed, while above it is longitudinally grooved for its entire length, and the edges of this groove are well curled outwards.

The maxillo-palatines are thin concavo-convex plates raised above the horizontal portions of the maxillaries, and otherwise arranged as in the Alcidæ and Laridæ.

The posterior heads of the palatines are in contact, and form a groove between them above for the rostral bar of the presphenoid. They are embraced in a peculiar manner by the anterior ends of the pterygoids, which are fashioned like little two-toed feet to hold them, the larger claw being above and the smaller one below, the seizure being of such a nature as to limit the motion to a fore and aft one. Coues noticed this arrangement in the loon, and alludes to it in his memoir. The posterior end of each pterygoid is much enlarged and makes an extensive articulation with the quadrate of the corresponding side.

The foramen ovale opens laterally in the red-throated diver, and still more so in the loon, and the posterior wall of each orbit is marked by an outwardly concave, nearly vertical ridge, which

seems to limit the depression of the crotaphyte fossa upon that aspect on either side. Among these divers the mandible is very much alike.

It is shaped so as to be in harmony with the form of the superior one, being carried to a sharp point anteriorly. Opposite to the posterior ends of the dentary each ramal side is deep from above, downwards, and the vacuity found in other birds upon this surface is completely closed in by the mandibular elements of the vicinity — the splenial and dentary — principally the latter.

As among the Alcidæ, however, we find a large elliptical foramen in the surangular in most divers, but rather a small one in the loon in the same situation. Both the upper and lower ramal borders are rounded and the coranoid processes fairly well developed.

Viewed from above, we find the mandible to be V-shaped, with rather a short symphysis. The articulate facets for the quadrate are large and included in a squarish area in each mandibular end. Each angle is truncate from above, downwards and backwards, its emarginated lateral borders behind, enclosing a rather deep concavity, seen upon direct posterior aspect. Now the outer of these two borders on either ramal angle is produced upwards, forwards, and outwards as quite a prominent peg-like process. Thus I consider the angles of this mandible as being both truncate and recurved, and it is easy to conceive how by gradual steps this condition in the Urinatoridæ could be so modified as to have the truncation subordinated or even disappear, while the process became the feature of the mandibular angle, as in such a form as *Lunda cirrata*, wherein but little further change is required to produce the process as found in the Gallinæ. The mandible of *Larus glaucus* before me has no such process, and the parts that give rise to it are not present, the mandibular ends being reduced to their simple requirements for articulation with the quadrates.

The skull and mandible in the Urinatoridæ are non-pneumatic, though apparently not always so in *U. imber*.

I regret very much to find that the hyoid arches belonging to the skeletons of these divers in my hands have been unfortunately lost, and I am unable to say anything about their struc-

ture in these birds from personal investigation. But in *U. imber* it essentially agrees with what we found in the grebes.

A complete skeleton of *Urinator lumme* (No. 13,646 Smithsonian Collection) before me, has 43 vertebræ in its spinal column. Of these the *fourteenth* is the first to bear a pair of free ribs; the succeeding six movable vertebræ connect with the sternum by costal ribs; the next seventeen unite as a "sacrum" with the pelvic bones; then follow six free caudals and a pygostyle containing several more.

The dorsal ribs are broad, and bear large, freely articulated epipleural appendages. Two pairs of ribs also come off from the sacrum, and meet long, sweeping hæmapophyses, that reach the costal borders of the sternum. This specimen has also a "floating costal rib," which is very small and delicate. It is seen on both sides. The form of the skeleton of the thoracic parietes agrees to some extent with the shape it assumes in the Alcidæ, with its hinder ribs sweeping beneath the pelvis. This latter bone is of extraordinary form and dimensions in all of the Urinatoridæ, even excelling the grebes in some of its peculiarities. The anterior portion of an ilium is short and depressed in comparison with its extensive backward reach. The neural crest of the sacrum appears above the pelvic bones for its entire length, and posterior to the large elliptical ischiac foramen the ilium looks directly outwards, then outwards and upwards. A small prepubis is present, while the post-pubic element is long and slender, its posterior extremity, curving beneath the pelvis behind, is dilated and paddle-shaped. It nearly meets the fellow of the opposite side, where both are completed by an emargination of cartilage. It differs from the grebes in that it articulates with the postero-inferior angle of the ischium upon either side.

Five of the last caudal vertebræ, together with the pygostyle, are shown in side view in my above mentioned paper (*Jour. Anat. and Physiol*). The three first chevron bones there exhibited are freely articulated over the joints of the centra when they are present; the ultimate ones, however, become anchylosed to the under side of the rear vertebra in each case, the last one really forming the antero-inferior process of the pygostyle.

Coues in his examination of the skeleton in *Urinator imber*

found 13 vertebræ in the cervical portion of the spinal column, with nothing especially peculiar in their articulations,[1] and he says that although they "possess characters which most readily separate them from those of any other portion of the column, they yet differ greatly from each other, in different portions of the neck..... Beginning with the third vertebra, and proceeding backwards, we find that the length of the bodies increases successively to about the 8th or 9th, when it again decreases rapidly, so that the last one is not as long as the third. The body of the third is thin, being exceedingly compressed vertically; and coincidently with the lengthening of each one successively to the 8th or 9th, they grow wider, and comparatively not so deep vertically; those that follow, however, do not again grow more compressed as they shorten; but on the contrary become broader and broader, so that the last one is as wide as deep, and very stout and strong. With this widening, there is also, towards the posterior extremity of this portion of the spine, a very high development of the transverse processes of the anterior extremities of each vertebra. This is so considerable, that the width across these transverse processes much exceeds the length of the whole vertebra. These processes are also exceedingly stout, with several roughened eminences for muscular attachments; and the foramen for the vertebral artery, which their two roots form, is as large as the spinal canal itself. Now as we proceed up the neck to the head, these transverse processes project less and less from the bodies of the vertebræ, and become less robust and angular, at the same time that they are antero-posteriorly elongated; and possess regular lamelloid walls, so as to form rather canals than simple foramina for the artery."

"The 'styliform processes' or 'rudimentary ribs' appear to arise from the posterior aspects of the summits of each of the transverse processes, beginning with the third vertebra. They are directed backwards, exactly parallel with the axis of the

[1] Coues, E., The Osteology of the Colymbus torquatus, with notes on its Myology.— *Mem. Bost. Soc. Nat. Hist.*, i, pt. ii, Nov., 1866, pp. 131–172, fig. 2, pl. 5. This time-honored and excellent paper was also afterwards separately issued with a slight change in its title, but apparently without revision.

column, and, according to their length, form a more or less complete osseous covering and protection to the vertebral artery during its passage between any two contiguous foramina."

Then after describing the neural and hæmal spines of the "cervical vertebræ"; the axis and the atlas, Coues proceeds by saying that, "If we consider the *dorsal* as corresponding in number with the ribs, we should assign ten to this portion of the column. The last three ribs, however, correspond to vertebræ which are completely anchylosed to the sacrum as well as to the iliac bones, and at the same time they differ in several respects from the dorsal ribs proper. . . . ."

"The transverse processes of these [dorsal] vertebræ are as usual very broad, long, and thin; their posterior border concave, their anterior convex, and their postero-external angles prolonged backwards into a short 'styliform' process, more or less intimately connected with the next succeeding vertebra. The horizontal lamellæ of the transverse processes of the last four vertebræ are pierced by a quite large foramen."

"The superior spinous processes of the vertebræ are so long that they nearly touch each other by their anterior and posterior borders; only a slight space being left between them. They are quite regularly rectangular in shape, having straight, flat superior borders at right angles with the anterior and posterior borders. They are connected with each other by dense and strong ligaments, and probably become more or less completely anchylosed with age." He then carefully describes the *enormous* development of the hæmal spines of the dorsal vertebræ,—and although of much the same shape, the one for *U. lumme* (*Jour. Anat. and Physiol.*) gives but a feeble idea of their remarkable development in *Urinator imber*, the subject of the memoir from which I have been quoting. Among themselves the motion of the vertebræ during life in this dorsal region of the column is wonderfully restricted, and as I have shown above, in some grebes the dorsal vertebræ all fuse into one common piece.

Coues made out 15 vertebræ as being fused together in the pelvic sacrum; but in a specimen before me, after careful count, there appear to be sixteen. Marsh found but 14 in the sacrum of *Hesperornis regalis*.

From specimens at hand it would appear that in *Urinator lumme*, the ilia anchylose with the sacral vertebræ for the entire length of the sacrum, whereas in a specimen of *U. imber* before me (No. 18256, U. S. Nat. Mus.) fusion only exists opposite the acetabulæ and thence on anteriorly to the fore end, inclusive. In Hesperornis it was only opposite the acetabulæ that fusion took place.

As much alike as the pelves of *U. lumme* and *imber* are, there is still another interesting difference between them, for in the former the anterior ends of the ilia are seen to be quite obliquely truncated, — they are more or less rounded in the latter species. Marsh says of those bones in *Hesperornis regalis*, that "the anterior extremity of the ilium is thin, and rounded in outline" (*Odontornithes*, p. 69), but fundamentally the pelves of all these divers are much the same.

In describing the ribs in *Urinator imber*, Coues remarks (p. 144) that they "are ten in number. Of these nine articulate with the spine, and eight with the sternum. Seven only are dorsal ribs proper; the eighth and ninth being articulated with the sacral vertebræ posterior to the tip of the crista ilii, and the tenth being connected neither with the spine nor sternum. . . ."

"As usual, the ribs consist of vertebral and sternal portions, movably articulated with each other. Both of these portions grow successively longer from before backwards; but the sternal portions much more rapidly than the vertebral. Thus while the sternal portion of the second rib is barely three fourths of an inch long, that of the seventh is fully three inches. The angle at the junction of these two portions, of course, varies with every stage of an inspiration and expiration; but at any given moment the angles become successively more acute from before backwards, — from the increasing length of the vertebral as well as the sternal portions. . . ." The last rib differs from all the others in being unattached at either vertebral or sternal extremity. It consists merely of two extremely slender elastic bones, tapering to a fine point, somewhat larger and broader at their bases, where they are joined to each other. The sternal portion is longer than the vertebral. Close by the junction of the two, this sternal portion sends off from its posterior border

a small, slight process, which curves directly outwards and forwards, lying parallel with the posterior border of the rib, which it joins again about an inch from its origin, — leaving a space filled up only by membrane. This may very possibly be regarded as the rudiment of an eleventh rib, of which the vertebral portion is wholly wanting. It is sometimes entirely obsolete."

"The latter ribs project so far backwards, that the thoracic parietes are prolonged some distance behind the acetabula, and consequently the femur in its normal position lies directly over the last three or four ribs, and moves backwards and forwards upon them. The angle of the last rib reaches within less than two inches of the posterior extremity of the elongated obturator foramen" (*loc. cit.* pp. 145, 146).

Marsh says that "the ribs of *Hesperornis* present no marked features to distinguish them from those of modern birds. They are composed of dense bone, but some of them contain irregular cavities. The articulated vertebral ribs of *Hesperornis regalis* are nine in number, on each side. The first three of these were attached to the last three cervical vertebræ, and had their distal ends free. The remaining six are all well developed ribs, which were connected by means of the sternal ribs with the sternum" (*loc. cit.* p. 63).

In comparing Marsh's figures of the sterna of *Hesperornis regalis* and *Hesperornis crassipes*, I find upon either costal border of the sternum of the first-named species but *four* facets for articulation with the costal ribs, whereas in the latter form there are *five* represented; and from this I am led to believe that there was quite as much, if not more, variation in this matter of ribs among those now long extinct types as there is among their existing affines. (Compare Marsh's Plates vi and vii, Figs. 1, 2, and 1, 2 respectively.)

Grebes, loons, and the great toothed divers of the Cretaceous period all vary in this particular. And sometimes, too, as we know, they are apt not to agree even in the number of facettes on the costal border of the same sternum. Frequently the number varies for the genus Urinator now under consideration, of the family Urinatoridæ, — sometimes in the same species, but more often among different species.

A clavicle of the pectoral arch has a broad head, but is as thin as a knife-blade, the outer aspect of which, when articulated, simply rests against the summit of the coracoid, while its posterior end rides over the head of the scapula. This expanded part of the clavicle rapidly contracts in width as it descends, until it becomes quite rod-like, square on section, to curve abruptly towards the sternum, where it unites with the fellow of the opposite side to support in the median line rather a long, peg-like hypocleidium. Viewed from in front, the furcula is a wide U-shaped bone, with its lower arc curved more than usually upwards. In common with other bones of the arch, it is non-pneumatic.

The lower part of a coracoid is much expanded laterally, with smooth and evenly concave articular lower margin for the sternal groove. As in some of the auks, the lower lateral margin of the bone develops a prominent upturned laminated process. The shaft of the coracoid is transversely elliptical on section, and its scapular process may, or may not descend, upon its inner side, sufficiently far as to be pierced by the foramen, which likewise occurs in the Alcidæ. The head rears to a considerable extent above the glenoid cavity, and its tuberous summit curls over towards the median plane.

Larus glaucus possesses a coracoid that has the foramen in the scapular process, as well as the laminated externo-lateral apophysis as in Urinator, but its furcula resembles that bone as we find it in the auks and guillemots.

The scapula in the red-throated diver is short, and doubly truncate behind. Its curvature may be quite abrupt just beyond the head in some specimens. This latter is transversely narrow, and thickened from above, downwards; it occupies the entire upper margin of the scapular process of the coracoid.

In the Yellow-billed loon (*U. adamsii*), when the pectoral arch is articulated *in situ*, if the line of the long axis of the coracoid were produced downwards, it would cut the lower margin of the keel of the sternum at the junction of its middle and anterior thirds; the scapulæ are much tilted upwards, and the aborted hypocleidium of the furcula is over the tip of the carinal angle and separated from it by about a centimetre.

In *Urinator imber* the U is by no means as broad as it is in *U. lumme*, the upper expanded parts are even still thinner, and relatively somewhat larger, and finally, it totally lacks the hypocleidium. All this agrees with the os furcula of the loon, the skeleton of which Coues described (*loc. cit.* p. 148).

The coracoid of *U. imber* very closely agrees with that bone as we find it in *U. lumme*, but the foramen that pierces the scapular process in *imber*, is a constant feature in that species. The scapulæ of these two divers are essentially quite alike, except in point of size. A point to be noticed in this latter bone, is the fact that the head and neck is bent at a rounded angle, with greater or less abruptness with the continuity of the blade of the bone. This flexure (*U. lumme*, Spec. No. 13646 coll. U. S. Nat. Museum) is greater in one scapula than it is in the other; the angle being more acute upon the left side. It is very open in other specimens.

In *Hesperornis regalis* the clavicles in the adult did not fuse with each other at the middle point below, simply articulating at the point of contact. This is the condition of those bones in the very young of *Urinator imber*, an embryonic condition, as it were, that persists throughout life in the great extinct ancestor of our loon.

Comparatively speaking, in all the loons, we find the sternum to be a very large bone. It is twice as long as it is broad, and it has great triangular costal processes. An extensive oval notch on either side of the keel behind gives rise to lateral xiphoidal processes, while the mid-portion, shaped like a shield or an escutcheon, extends considerably more posteriorly, and does not entirely ossify around its hinder border until late in life. It may be pierced by a few foramina, where ossification has not been quite thorough. This part of the sternum is unkeeled, the keel at the best being very low, but with prominent and projecting carinal angle in front.

As I have said above, the usual number of facets upon either costal border is eight; there may, however, be but seven. The manubrium is broadly wedge-shaped and nearly aborted; its triangular, anterior face is slightly concaved. Costal grooves are long and deep, but relatively, not as deep as they are in the

grebes. They almost meet each other in the middle line, the interval between them being less than the width of manubrial base. On its thoracic aspect the bone is concaved, being most so anteriorly, and gradually shallowing as we approach its hinder part. Both this surface and the ventral one are very smooth. Upon the latter the 'pectoral muscular line' extends from the mid point of the lower lip of the outer third of the costal groove obliquely to the carina meeting it at the juncture of its anterior and middle thirds. In *U. imber* the bone averages 20 centimetres for its greatest length, and 8.5 cms. for its greatest breadth; — the last measurement being taken across the lateral xiphoidal processes. Though very light and elegantly proportioned the base is absolutely non-pneumatic throughout the superfamily. Its form is well shown in the sternum of *Urinator lumme* (Spec. No. 16628 of the U. S. Nat. Mus. Coll. ♀) but its pattern may vary considerably, being remarkably narrow and long in some individuals. When thus fashioned it reminds one very much of the sternum in certain of the auks. But among some water birds skeletal characters crop out very strangely sometimes, and even to the casual observer the sternum of an albatross, a cormorant, Plotus, a fulmar, and a grebe all more or less closely resemble each other upon a direct pectoral view, and to a less extent in several of those forms, when viewed from the side.

In concluding his account of the sternum of the loon, Coues says: "Viewing, now, the sternum as a whole, we have to notice how great an extent of surface is secured with a trifling increase of weight. Posteriorly, this is attained by means of the great lateral projection of the apophyses, as well as by their length, and by the breadth and projection backwards of the thin, almost cartilaginous xiphoid. Anteriorly, where the sternum is not so wide, the deficiency is atoned for by the great depth of the keel, and its projection forward; at the same time the outline of the crest of the keel is such that when the inequalities of the bone is all filled up with muscular tissue the resulting surface becomes flat, and broad as well as long, affording the best possible outline for contact with the water." (*loc. cit.* pp. 147, 148.)

According to Marsh "The sternum in *Hesperornis* somewhat

resembles in general form the corresponding bone in the genus *Uria*, but in other respects is more like that in the *Ratitæ*. It is thin and weak, and entirely without a keel. It is expanded in front, especially between the costal processes, and has two deep grooves for the reception of the coracoids. These grooves are placed obliquely, converging anteriorly, and are widely separated from each other. The sternum has a rounded mesial projection in front, which is somewhat thickened, but there is no true manubrium." .... "The sides of the sternum in *Hesperornis* are concave in outline, and in *Hesperornis regalis*, there are four articular projections on each side for the attachment of sternal ribs. These processes are all on the anterior half of the sternum. Behind these the lateral margins are nearly parallel. The posterior end of the sternum is quite thin, and had two shallow emarginations. In *Hesperornis crassipes* the sternum had five articular faces on each side for the sternal ribs. The posterior margin in the same species is less excavated than in *Hesperornis regalis*." (*Ordontornithes*. p. 60.)

If you will refer to Plate VII of Marsh's work, from which I have just been quoting, and examine Fig. 3 of the sternum of *Hesperornis crassipes*, it will not be difficult to believe that perhaps the sternum of that species had lateral xiphoidal processes something like those found in *Colymbus cristatus*. In the specimen they look very much as though they had been broken off, an accident very likely to occur in the sternum of a fossil bird, and frequently seen even in the sterna of our existing birds in the collections in the museums. The xiphoidal part of the sternum was cleft by a shallow triangular notch, in *Hesperornis crassipes*, precisely as we find it now in many of our existing grebes.

THE PECTORAL LIMB IN THE URINATORIDÆ.

All the bones of the upper extremity are non-pneumatic in this family. They are heavy, and when simply cleaned in the rough, they soon become dark and the oily substances contained in their cavities ooze out upon their outer surface in no inconsiderable amount.

The palmar aspect of the proximal end of the humerus has a large subcircular elevation upon it that is quite characteristic. This projects in such a manner that upon the reverse side it is seen extending beyond the border of the bone, near the shallow, pseudo-pneumatic fossa.

The radial crest from its size and length is more than usually conspicuous; its free border is a long convexity, and this plate-like process is carried well down the shaft, occupying fully one-third of its length. Below it, the shaft for its middle third becomes subcylindrical, showing a large nutrient foramen upon its ulnar aspect.

The distal end of the bone is not spread much in a transverse direction, but otherwise rather bulky. Two wide and shallow furrows mark it on the anconal side for the passage of tendons, and a large oblique and ulnar trochlea stand out upon the other. The ectocondyloid process is barely noticeable.

The radius is straight, and the major part of its shaft nearly cylindrical; its articular ends present the characters of the bone as seen in the majority of the class. When articulated, these alone meet the ulna, giving rise to a long, narrow, interosseous space. Towards this the larger bone of the antibrachium presents a concave border of a moderate degree of curvature. Its shaft, too, is quite cylindrical, and faintly shows the row of papillæ for the quills of the secondaries. It develops in a transverse direction not an inconsiderable ledge at its distal end, upon which the expanded end of the radius rests in articulation.

The carpus is composed of the two elements found in most birds; they are here simply somewhat modified in form for the family, and to accommodate themselves to the shape of the other bones with which they come in contact. They in turn having their own specific cast.

One of the first things that forces itself upon our attention in examining the skeleton of the hand of one of these divers is the unusual length (comparatively speaking) of the metacarpals. Of these, the one for the pollex digit is of an extraordinary length; much more than a third the length of the index one, and co-ossified with it in the usual manner.

I do not recall an instance among birds where the comparative

lengths of these two metacarpals is anything like it. The proximal phalanx of the pollex is also long and compressed. It bears a claw upon its extremity. Both of the other metacarpals are long and very straight, allowing but a narrow interval to exist between them.

The blade of the proximal phalanx of the index is meagre, being flat anconad and faintly pitted upon the opposite side. Its distal joint also bears a claw.

The phalanx of the middle finger is fully half as long as the expanded one of index alongside of which it lies.

These observations upon the pectoral limit of the Urinatoridæ have been jotted down during my examination of this part of the skeleton in a specimen of *U. lumme*, and in it I find the skeleton of the manus, just described, equalling in length the bones of the antibrachium.

The humerus in this diver has a length of about 14.5 cm.; the radius 11.4; the ulna 11.65; manus 11.8, of which latter the carpo-metacarpus claims 7.5 cm. From this it is seen that when the skeleton of the limb is in a position of rest and closed alongside the chest, the humerus projects beyond the bones of the anti-brachium for some little distance. This is not the case among the Laridæ, whereas it agrees with *Alca torda*, Uria, and, I expect, the Alcidæ generally.

The Pelvic Limb in the Urinatoridæ.

The skeleton of the pelvic limb in the Urinatoridæ is a very interesting structure, and highly characteristic of the family.

Coues has described its mechanism and structure in *U. imber* in his memoir before alluded to, and I will here record a few observations that I have made upon this limb as found in *Urinator lumme*.

The femur is short and thick, being about as long as the cnemial process of the tibio-tarsus above the articulation. Its short shaft is somewhat cylindrical near the middle, bowed to the front, and scarred in many places by tuberous projections for muscular insertion. The head is large and globular, sessile, and deeply marked by the pit for the ligamentum teres. Dis-

tally, it is much expanded in a transverse direction, the inner condyle being small and elevated, the outer one being very large, strongly cleft behind for the fibular head, much the lower of the two, and separated from its companion in front by a deep rotular fossa.

The patella of the red-throated diver and other loons is generally considered to be the flake-like bone articulating at the posterior base of the cnemial process of the tibia. Its form and exact position I have given in my paper on the patellæ in birds referred to in the second paragraph of the present paper. This illustration also presents the outer aspect of the femur, tibio-tarsus, and fibula; the latter two for their proximal two-thirds only.

Nothing could be more interesting than the form assumed by the tibio-tarsus of this diver. Its cnemial process is enormously produced, having a deep, longitudinal concavity between its pro- and ecto-cnemial ridges in front, and the two sides meeting in a median ridge behind. The pro-cnemial ridge is carried down as a wing for some distance on the side of the shaft. This latter is somewhat flattened from before backwards for its entire length, but better marked in this particular at its distal extremity, just before we arrive at the condyles, where also it is marked by the broad, shallow tendinal groove. This is bridged over by the usual bony span for the deep extensors.

The condyles are very prominent in front, but approach each other as low, sharp ridges behind. Coues found the fibula in the loon, "for an inch or so, quite separate from the tibia; is then united with it for some distance, becomes again distinct for about an inch, and then finally merges as a slender spiculum into the side of the tibia, rather more than an inch above the joint. A slight crest, however, gives an indication of it, which can be traced quite to the external malleolus of the tibia." This description agrees with one of the specimens of *U. lumme*, but in another it is carried down distinct and prominent to terminate in a well-formed malleolus upon the lower antero-lateral aspect of the shaft. The lower portion is anchylosed with the tibio-tarsus, but could, with but little difficulty, be separated from it with a good sharp knife. In other words we find specimens of *Urinator lumme* wherein the fibula is complete.

Four figures of the Plate illustrating the present paper are devoted to the extraordinary tarso-metatarsus of the Urinatoridæ as seen in *U. lumme*. These give various aspects of the bone, and distinctly show all the characters it possesses. Chief among these is the great amount of lateral compression of the shaft and trochlear end. The former is grooved both in front and behind for its entire length, forming a guide as well as a harbor for the passage of tendons.

The hypotarsus is very large, it being composed of a posterior arcade of bone with three distinct foramina piercing its substance in front of it. Occupying a position above the base of the mid-trochlea, the inner one of these three compressed protuberances projects the most posteriorly. The remaining two are separated by a cleft, which is continued above by a groove on the anterior surface, to be pierced obliquely from above, downwards, by the usual arterial foramen. The mid-trochlea is the lowest of all three, and rather the most anterior. They are all strongly marked by median grooves intended for the corresponding surface on each proximal phalanx of the digits.

A scale-like first metatarsal is suspended by a ligament attached to its entire anterior free border, to the inner inferior posterior margin of the shaft of the bone. It supports a feebly developed phalanx and claw representing the hallux digit. As for the three anterior toes, they are composed upon the usual formula for the number of joints as found in this member in the majority of the class. All of the ungual phalanges are in this diver flat and scale-like.

The proportionate lengths of these joints in the skeleton of the pes are shown in the following measurements: — Hallux joint has a length of but 1.1 centimeters, its claw but 0.5; the proximal phalanx of the inside toe measures 4.0 centimeters, the next joint 2.1, and its claw 0.95. The proximal joint of the middle toe 3.6, next joint 2.0, next 1.8, the claw 0.9; finally the proximal joint of the outside toe 2.8, next 1.6, next 1.4, next 1.8, and the claw 0.85.

Aside from the osteology and other interesting points of structure in the pelvic limb of red-throated diver, a notable feature is to be noticed in the great number of fibrous loops

attached to the long bones at a number of points, which serve to surround and guide the various tendons on their passage to the toes and prevent them from slipping from their places as they pass these narrow bones, when the limb is brought into vigorous action.

D'Arcy Thompson in his very excellent memoir "On the Systematic Position of Hesperornis" in contrasting the characters presented in the pelvic limb of *H. regalis* with the corresponding ones as found in the hind limb of *U. imber* says of the former that "Firstly, the extreme shortness of the femur is a very Colymbine feature; that bone is in *Colymbus* [*Urinator*] and *Hesperornis* about one-quarter the length of the ilium; whereas in the Ratites, except in exceptional cases, such as *Dinornis elephantopus*, the two bones are nearly of equal length. Secondly, and of greater importance, the patella, which, small and double in the Ostrich, is rudimentary or absent altogether in the other Ratites, is of immense size and peculiar shape in *Hesperornis*. In this bird it is a long trihedral pyramid, pointed at its superior extremity, concave on its outer surface, bearing at its lower extremity special and separate articular surfaces for the tibia and femur, and lying in a line with the long axis of the femur. Except that it is perforated for the tendon of the *ambiens* muscle (as in the Gannet), it is extremely like the patella of the Grebe, and practically identical with that of *Colymbus* [*Urinator*], except that in this latter it is fused with the upper extremity of the tibia. The existence of a small additional sesamoid in the knee-joint of *Colymbus* [Urinator] (Owen, *Comp. Anat. II.*, p. 83) does not invalidate the homology here adopted of the long 'rotular process of the tibia' with the patella." (pp. 11, 12.)

If Thompson means by this that in the loons (Urinator) the patella originally was separate as it now is in the grebes and held the same relative position to an elongated rotular process of the tibio-tarsus, as in the latter birds, and that since, in the loons, such a patella has come to be fused with the aforesaid process of the tibio-tarsus, the present writer is inclined to agree with him, although he formerly held the opinion that the small flake-like bone described by Owen was the only patella possessed

by the Urinatoridæ. Further along I shall refer to this matter again.

The study of the patella in birds is a very interesting, not to say, an important one, and, as has been noted above, as long ago as 1884 the writer published an article in the *Proceedings of the United States National Museum* on the subject (Vol. VII, pp. 324–331) in which was figured the patellæ of certain penguins, mergansers, gannets, grebes, divers, fulmars, Hesperornis, crows and cormorants; and to that article the reader is referred for information touching what has just been said above.

There can be no question about the existence of the patella in the grebes, nor in Hesperornis, nor in the cormorants, but as I have already shown, morphologists are not thoroughly agreed upon the nature of the flake-like sesamoid found at the knee in a loon, nor homologically speaking, its significance. Granted that a large patella in the Urinatoridæ has fused with the long cnemial process of the tibio-tarsus, then it would hardly appear that the small flake-like bone in the tendon of the extensor femoris muscle should be considered a patella at all, although in the matter of position it agrees with that sesamoid as it is found in all birds that possess it. It would hardly seem reasonable that Urinator had *two* patellæ at either knee-joint, and such very dissimilar ones. In my opinion the last word upon this subject remains yet to be said. The embryology of the Urinatoridæ, as well as the morphology of the structures involved in specimens of nestlings and subadults of the species in all stages of their growth, requires investigating.

In the *Journal of Anatomy* (London) (Vol. XXIV, January, 1890, and other volumes) I published a "Brief Summary of the Principal Osteological Characters of the Urinatoridæ" to which I refer the reader for further details regarding the osteology of the grebes and loons.

It now remains for me to compare the principal osteological characters of the loons and the grebes. These may be conveniently arranged for reference in the following manner:—

A FEW OF THE OSTEOLOGICAL CHARACTERS WHICH DISTINGUISHED THE PODICIPOIDEA AND THE URINATOROIDEA.

Podicipoidea.— Pars plana ossifies.

Urinatoroidea.— Pars plana does not ossify.

Podicipoidea.— Supra-orbital glandular fossæ but faintly mark the skull.

Urinatoroidea.— Supra-orbital glandular fossæ deeply mark the skull, being within the superior border of the orbit and separated from each other mesially by a *thin*, longitudinal crest of bone.

Podicipoidea.— Twenty-four (24) or more dorso-cervical vertebræ.

Urinatoroidea.— Twenty (20) dorso-cervical vertebræ. Not more.

Podicipoidea.— Sternum *short* and broad, with the lateral xiphoidal processes extending more posteriorly than the mid-xiphoidal piece, which latter is triangularly notched in the middle line.

Urinatoroidea.— Sternum nearly twice as long as it is broad, with the lateral xiphoidal processes not extending more posteriorly than the mid-xiphoidal piece, which latter is unnotched and rounded off posteriorly.

Podicipoidea.— Posterior free extremities of *os furcula* very narrow and pointed.

Urinatoroidea.— Posterior free extremities of *os furcula* very broad, laterally compressed, and apices bluntly rounded off.

Podicipoidea.— Posteriorly the ischium does not articulate with the superior margin of the very long post-pubic style, anterior to its free end; and the latter is not perceptibly dilated.

Urinatoroidea.— Posteriorly the ischium does articulate with the superior margin of the very long post-pubic style, anterior to its free end; and the latter is considerably dilated and paddle-shaped.

Podicipoidea. — Pollex metacarpal short.

Urinatoroidea.— Pollex metacarpal remarkably long.

Podicipoidea.— Possessed of a large patella, co-existing with an elongated cnemial process of the tibio-tarsus.

Urinatoroidea.— Possessed only of a very small, flake-like sesamoid, which occurs in the tendon of the extensor femoris muscle at its insertion; and probably the true patella has coössified in the adult with the elongated cnemial process of the tibio-tarsus.

AFFINITIES OF THE PYGOPODES.

Taken in connection with many other good characters presented in the structure of grebes and loons, we must believe that the differentiating osteological ones just given above, point to the fact that the relationship now existing between these two well-defined groups of birds can best be appreciated by creating for them a superfamily in each case. To this end I consider the grebes to compose the superfamily Podicipoidea, and the loons the superfamily Urinatoroidea.

In 1884 (*Proc. U. S. Nat. Mus.*, vol. vii, p. 331) I considered the representatives of the extinct genus of cretaceous toothed birds, Hesperornis to be "powerful divers" and the "ancient ancestors" of our present existing grebes and loons. Essentially, this still remains my opinion; and, at a later day, after carefully comparing the osteological characters of the Podicipoidea and Urinatoroidea with the corresponding ones in the skeleton of *Hesperornis regalis* and *H. crassipes* as given by Marsh, I again said that the result of those investigations "convince me of the fact that, however widely separated now, our existing loons and grebes are derived from the same ancestral stock to which *H. regalis* belonged" (*Jour. of Anat.* London, Jan., 1890, p. 169).

Our existing grebes and loons then are derived from, or are the descendants of great toothed divers long since extinct. Possibly the Hesperornithidæ were an offshoot family of a superfamily,—the Hesperornithoidea, the latter the more typical of these extinct divers, and from them our present Pygopodes were derived, but we yet lack the necessary material to place such a question beyond dispute. From a consideration of the osteolog-

ical characters I consider the Podicipoidea to be an earlier offshoot of the pygopodine stem than the Urinatoroidea, and more nearly related to Hesperornis than are the latter birds. The morphology of the pelvis and the pelvic limb, as well as certain characters in the skull and trunk skeleton, point, I think, in favor of this view.

No doubt but what the Hesperornithidæ were in their turn derived from still more ancient ancestors possessed of the power of flight, and in the ages to come our present-day Pygopodes, if it be their fate to have descendants, direct or indirect, those descendants may in turn again become flightless forms through a gradual loss of their pectoral limbs.

So far as the affinities of the Pygopodes are concerned with other groups of existing birds, we shall see in other memoirs I propose to publish on the subject that they present a number of osteological characters exhibited in common with the Alcæ and the Longipennes.

EXPLANATION OF THE PLATE.

(Limb-bones of Water Birds: all drawn by the author, about five-sixths natural size.)

FIG. 1. Right femur of *Urinator lumme*; anterior surface.

FIG. 2. Right femur of *Urinator lumme*; inner surface.

FIG. 3. Right tarso-metatarsus of *Larus delawarensis*; anterior aspect.

FIG. 4. Right tarso-metatarsus of *Larus delawarensis*; distal extremity viewed from below.

FIG. 5. Right tarso-metatarsus of *Larus delawarensis*; proximal extremity viewed directly from above; nat. size. Figs. 3, 4, and 5, all from the same specimen.

FIG. 6. Right tarso-metatarsus of *Hæmatopus bachmani*; anterior aspect.

FIG. 7. Direct view from below, distal extremity, same bone as in Fig. 6.

FIG. 8. Direct view from above, proximal extremity of the right tarso-metatarsus of *H. bachmani*, same bone as shown in Figs. 6 and 7.

FIG. 9. The same bone as in last figure seen upon the inner aspect of its distal extremity. (All from specimen 13636, coll. U. S. Nat. Mus.)

FIG. 10. Right tarso-metatarsus of *Chiornis minor*, anterior aspect. (From Dr. Kidder's type specimen.)

FIG. 11. Direct view from above, proximal extremity, same bone as in last figure.

FIG. 12. Direct view from below of the distal extremity of the right tarso-metatarsus of *Chiornis minor*.

FIG. 13. Right femur of *Chiornis minor*; anterior surface.

FIG. 14. Right femur of *Hæmatopus backmani*; anterior surface. (No. 13636, coll. U. S. Nat. Mus.)

FIG. 15. Right femur of *Larus delawarensis*; anterior surface.

FIG. 16. Right tarso-metatarsus of *Urinator lumme*; inner surface.

FIG. 17. Right tarso-metatarsus of *Urinator lumme*; anterior surface. Same specimen.

FIG. 18. Direct view from above, proximal extremity, of the same bone (*U. lumme*).

FIG. 19. Right femur of *Urinator lumme*; posterior surface.

FIG. 20. Direct view from below of the right tarso-metatarsus of *Urinator lumme*, distal extremity.

FIG. 21. Right tibio-tarsus and fibula of *Urinator lumme*; anterior aspect.

FIG. 22. Right tibio-tarsus of *Chiornis minor*.

FIG. 23. Right tibio-tarsus and fibula of *Hæmatopus backmani*; anterior surface. (No. 13636, Coll. U. S. Nat. Mus.)

FIG. 24. Right tibio-tarsus and fibula of *Larus delawarensis*; anterior surface. From the same skeleton that furnished bones for the other figures given above.

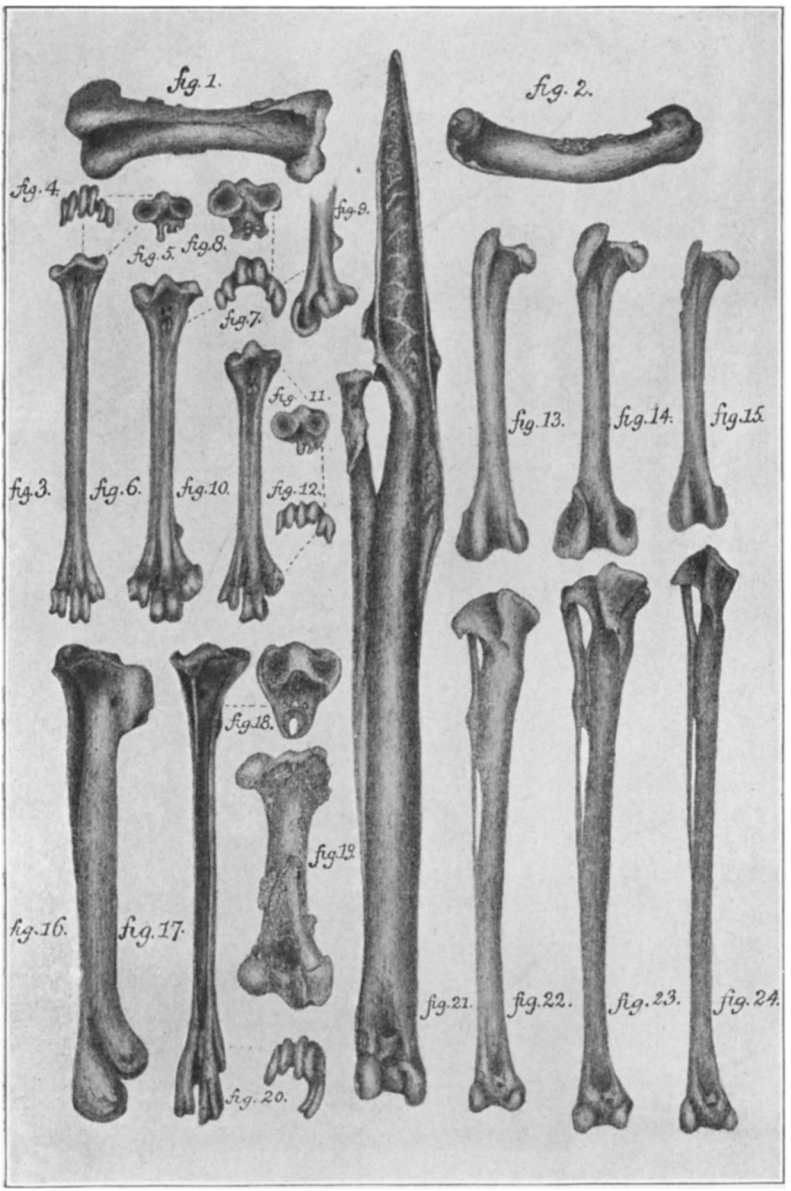
fig. 1.
fig. 2.
fig. 4.
fig. 5.
fig. 8.
fig. 9.
fig. 7.
fig. 11.
fig. 12.
fig. 3.
fig. 6.
fig. 10.
fig. 13.
fig. 14.
fig. 15.
fig. 18.
fig. 19.
fig. 16.
fig. 17.
fig. 20.
fig. 21.
fig. 22.
fig. 23.
fig. 24.